

Interlimb Coordination, Gait, and Neural Control of Quadrupedalism in Chimpanzees

LIZA J. SHAPIRO,^{1*} FRED C. ANAPOL,² AND WILLIAM L. JUNGERS³

¹*Department of Anthropology, University of Texas at Austin, Austin, Texas 78712*

²*Department of Anthropology, University of Wisconsin, Milwaukee, Wisconsin 53201*

³*Department of Anatomical Sciences, SUNY at Stony Brook, Stony Brook, New York 11794*

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ABSTRACT Interlimb coordination is directly relevant to the understanding of the neural control of locomotion, but few studies addressing this topic for nonhuman primates are available, and no data exist for any hominoid other than humans. As a follow-up to Jungers and Anapol's ([1985] *Am. J. Phys. Anthropol.* 67:89-97) analysis on a lemur and talapoin monkey, we describe here the patterns of interlimb coordination in two chimpanzees as revealed by electromyography. Like the lemur and talapoin monkey, ipsilateral limb coupling in chimpanzees is characterized by variability about preferred modes within individual gaits. During symmetrical gaits, limb coupling patterns in the chimpanzee are also influenced by kinematic differences in hindlimb placement ("overstriding"). These observations reflect the neurological constraints placed on locomotion but also emphasize the overall flexibility of locomotor neural mechanisms. Interlimb coordination patterns are also species-specific, exhibiting significant differences among primate taxa and between primates and cats. Interspecific differences may be suggestive of phylogenetic divergence in the basic mechanisms for neural control of locomotion, but do not preclude morphological explanations for observed differences in interlimb coordination across species. *Am J Phys Anthropol* 102:177-186, 1997 © 1997 Wiley-Liss, Inc.

The neural control of locomotion has been studied in detail across a wide variety of animals (e.g., Delcomyn, 1980; Vilensky, 1987; Swinnen et al., 1994). Such research has supported the existence of central pattern generators, or CPGs. Central pattern generators for locomotion are groups of neurons located in the spinal cord that, in many species, can produce rhythmic patterns of limb movements even when isolated from sensory inputs (e.g., Miller et al., 1975; Miller and Scott, 1977; Grillner, 1975, 1979; Delcomyn, 1980; Selverston, 1980; Grillner and Wallén, 1985; Cohen et al., 1988). The functioning of locomotor CPGs has been

explored through a variety of methods including the study of interlimb coordination, or timing of the locomotor cycles of the limbs in relation to one another (Afelt and Kasicki, 1975; Coss et al., 1978; English, 1979, 1980, 1989; English and Lennard, 1982; Swinnen et al., 1994). Initial studies in this area emphasized the functioning of CPGs exclusive of supraspinal input or external cues from changing environments. For instance, cats were found to employ very rigid pat-

*Correspondence to: Liza Shapiro, Department of Anthropology, University of Texas at Austin, Austin, TX 78712-1086.

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terns of interlimb coordination, regardless of environmental cues (e.g., Miller et al., 1975; Miller and van der Meché, 1976). However, CPG function is largely facilitated by outside input, from the environment and/or supraspinal neural information (Coss et al., 1978; Eidelberg et al., 1981; Pearson, 1987; Harris-Warrick and Johnson, 1989; Smith et al., 1993). For example, quantification of the timing and coordination of limb pairs in cats reveals preferred modes, but with substantial variability (Coss et al., 1978; English, 1979, 1989), reflecting "the facultative capabilities of the neural mechanisms controlling locomotion" (English 1979, p. 229).

Although a great deal of research has been dedicated to the functional morphology and evolution of primate gait, little pertains to primate interlimb coordination and its relationship to neural control (but see Vilensky, 1983, and Vilensky and Patrick, 1985). Jungers and Anapol (1985) carried out such a study on *Lemur fulvus* and *Miopithecus talapoin* using electromyography of limb muscles. Electromyographic analyses of interlimb coordination complement those using footfall patterns or limb joint angles, but electromyographic data may provide a more direct reflection of neural output (Grillner, 1975; Coss et al., 1978; English, 1979, 1980; English and Lennard, 1982). Jungers and Anapol (1985) found that interlimb coordination patterns in the lemur and talapoin monkey, like those reported for cats, displayed variability about a central tendency or "preferred" mode, expressing both the constraint and flexibility of neural control mechanisms. The same was true when walking and galloping gaits were examined separately in these two primates, and to some extent, preferred modes appeared to be species-specific. Jungers and Anapol (1985) also noted differences in modal patterns between primates and those reported for cats (see Discussion).

Interlimb coordination of primates is further investigated here in the common chimpanzee (*Pan troglodytes*) using electromyography. A chimpanzee's interlimb coupling patterns would be expected to differ from those of a lemur or talapoin monkey, especially given the chimpanzee's more versatile

locomotor repertoire and suspensory anatomy (as reviewed in Hunt, 1991, 1992; Doran, 1993). This study also tests further the hypotheses that (1) within gaits, interlimb coordination patterns are variable, but exhibit a "preferred" mode; (2) interlimb coordination patterns of primates are species-specific, and differ from those of other mammals, specifically cats.

MATERIALS AND METHODS

Data on ipsilateral limb coordination were collected using telemetered electromyography. The subjects were two young adult male chimpanzees walking, running, and galloping quadrupedally on a flat, smooth floor in an enclosure measuring $7.3 \times 3.7 \times 2.7$ m. Details of the experimental environment have been described elsewhere (Jungers et al., 1980, 1983). Data were collected from the two subjects in separate recording sessions. With the animals under halothane/nitrous oxide anesthesia, fine-wire bipolar electrodes were inserted into triceps brachii (lateral head) and vastus lateralis, and each muscle was monitored simultaneously on both sides. For vastus lateralis, the electrode was placed mid-belly. For triceps brachii, the lateral head was pinched up and separated from the long head, and the electrode was placed centrally in the longitudinal bundle of the lateral head. Location of electrodes was verified by back-stimulation to elicit a contraction in the muscle of interest. Triceps brachii and vastus lateralis are extensors of the forelimb and hindlimb, respectively. They are active during support phases of the limbs in order to prevent collapse of the elbow and knee joints into flexion due to the force of gravity (Tokuriki, 1973; Rasmussen et al., 1978; English, 1979; Jungers et al., 1980, 1983; Jungers and Anapol, 1985). Their activity patterns are therefore good indicators of the timing of limb movements relative to one another.

Using the triceps brachii as the reference muscle, *phase intervals* were calculated as the ratio of *latency* to *step duration* (following English, 1979, and Jungers and Anapol, 1985; see Fig. 1). Latency is the duration of time from termination of electrical activity in the reference forelimb (triceps) to termination of activity in the ipsilateral hindlimb

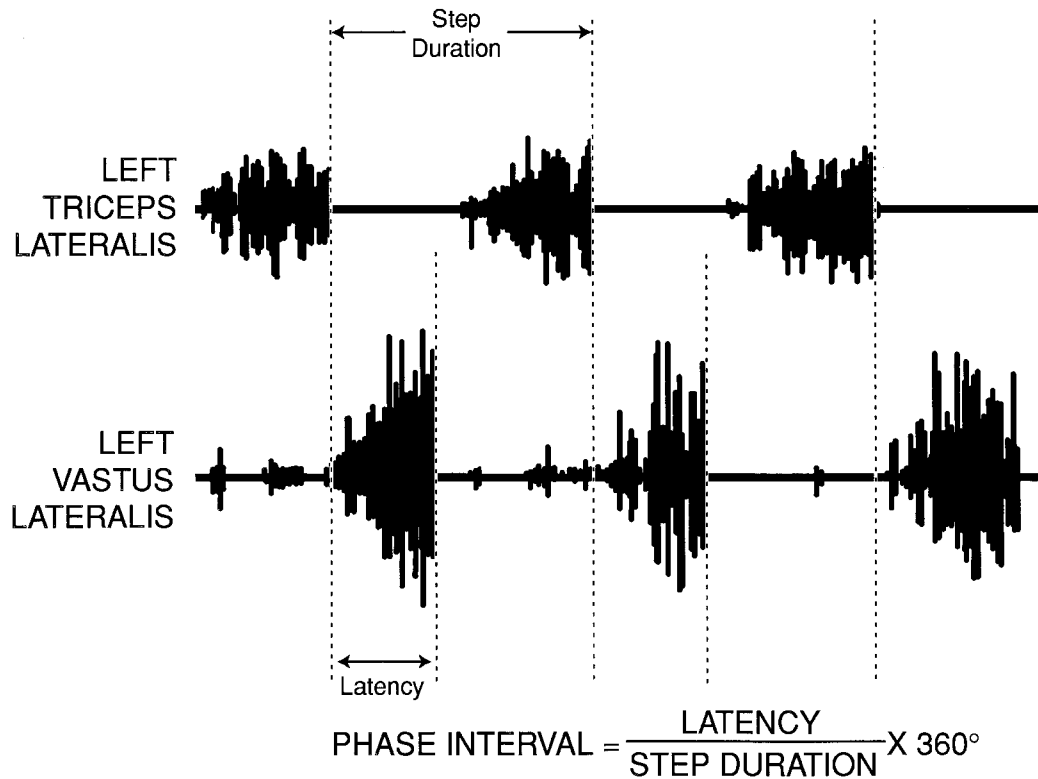


Fig. 1. Raw electromyograms from the left triceps lateralis and left vastus lateralis of Chimpanzee 1, depicting the method by which phase intervals were defined and measured in the study (Jungers and Anapol, 1985). Both muscles are active during the support phase of the limb.

(vastus lateralis). Step duration (equivalent to stride or phase duration) is the period of time between termination of electrical activity in the reference forelimb muscle (triceps) to subsequent termination in the same muscle. In order to represent their potentially continuous distribution, phase intervals were translated into degrees by multiplying the quotient of latency and step duration by 360° (English, 1979). Phase intervals can therefore range from 0° to 360° . For example, a phase interval of 180° would indicate that activity in the vastus lateralis terminates halfway through the successive terminations of activity in the triceps on the same side, i.e., the two muscles/limbs are exactly out of phase (as in a trot). By contrast, an interval of 0° or 360° corresponds to ipsilateral muscles/limbs completely in-phase (as in a pace) (English, 1979, 1989).

Although the data reported here are restricted to those based on the forelimb as the reference limb, equivalent results were found using the hindlimb as the reference limb. Likewise, data are reported for the left side ipsilateral limbs only, because very similar results were found for the right side ipsilateral limbs. Phase intervals in the two chimpanzees were examined as a function of both phase duration (which is inversely related to speed) and gait category. Gaits were characterized as either symmetrical (walk/run) or asymmetrical (gallop) following the terminology developed by Hildebrand (1966, 1967). Special attention was also paid to "overstriding" in chimpanzees; symmetrical gaits were separated into "hindlimb-inside" forelimb and "hindlimb-outside" forelimb (Hildebrand, 1967, 1968, 1976; Reynolds, 1985; Larson and Stern, 1987; Demes et al., 1994).

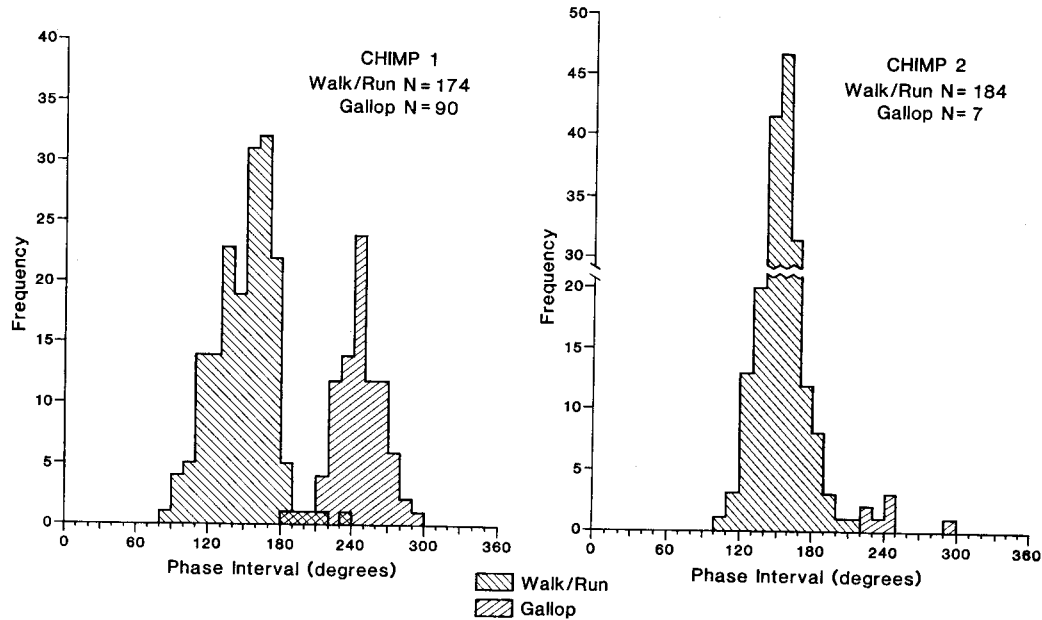


Fig. 2. Frequency distributions of phase intervals for the two chimpanzees, separated by gait category. Walk and run are symmetrical gaits, and gallop is an asymmetrical gait.

Nonparametric statistics were used to test for intra- and interspecific differences in phase interval distributions. More specifically, the Mann-Whitney U-test was used to assess locational differences in phase interval distributions (1) of symmetrical gaits between Chimpanzee 1 and Chimpanzee 2; (2) between hindlimb-inside and hindlimb-outside symmetrical gaits within each chimpanzee; (3) between symmetrical and galloping gaits in the chimpanzee with the most gallops; and (4) of symmetrical gaits among chimpanzee, lemur, and talapoin monkey. A Kolmogorov-Smirnov two-sample test was used to test for differences in phase intervals between symmetrical gaits of primates and the values figured for cats (cat data from English, 1979).

RESULTS

Phase intervals

Figure 2 depicts the frequency distributions of phase interval values in each chimpanzee during both symmetrical (walk/run) and asymmetrical (gallop) gaits. Phase interval patterns are easily distinguishable with little overlap between the two types of gaits. The results are very similar for both chimpanzees,

notwithstanding the fact that the second chimpanzee did not gallop as frequently as the first. The modal intervals for symmetrical gaits (walk/run) range from 150–170° (160–170° in Chimpanzee 1, 150–170° in Chimpanzee 2), and the modal intervals for galloping range from 240–250°. The differences in pooled walk/run phase intervals between the two chimpanzees are not significant ($P > 0.25$), but the differences between symmetrical and asymmetrical phase intervals are significant ($P < 0.001$, tested for Chimpanzee 1 only).

The distinction in phase interval values between gait types can also be seen when phase intervals are plotted against phase duration (Fig. 3). Overall, longer phase durations (slower speeds) are associated with “walk/run” phase intervals, while “galloping” intervals occur at shorter phase durations (faster speeds). Both types of gaits are used at 500–650 msec, but the gait-associated phase intervals remain distinct. However, *within* symmetrical gaits (walk/run), phase intervals show no correlation with phase duration, and phase intervals of asymmetrical gaits show only a weak negative

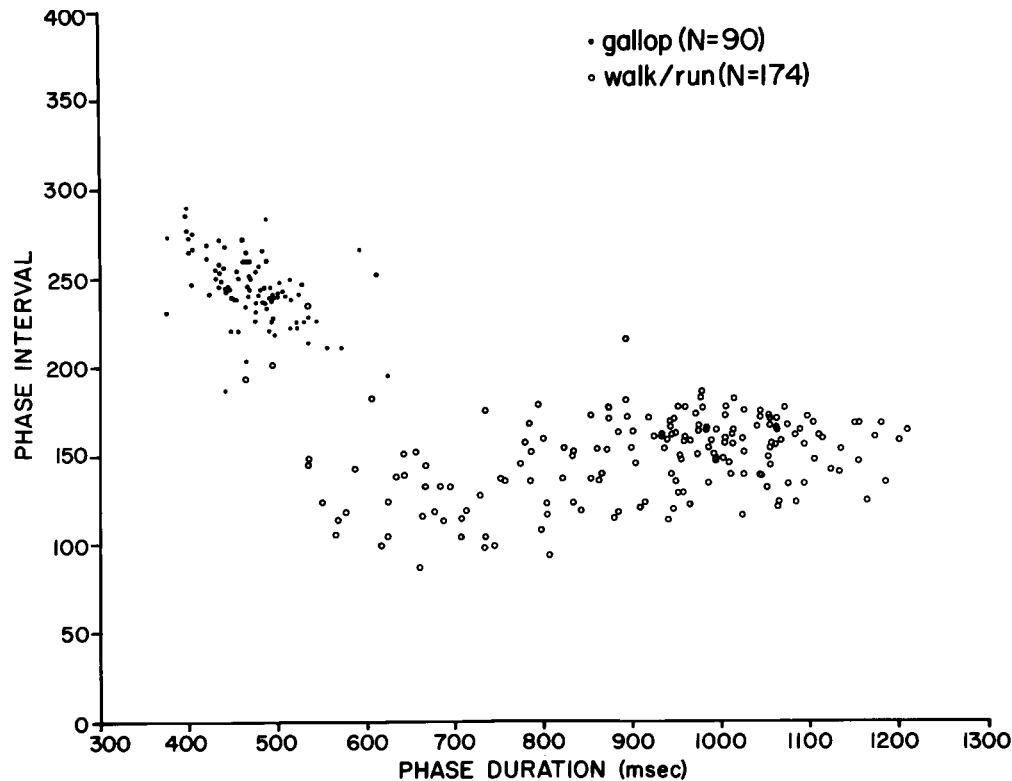


Fig. 3. Phase intervals as a function of phase (step) duration in chimpanzee 1. Phase duration is inversely related to speed.

correlation with phase duration. Therefore, while differences in phase intervals *between* gaits may be speed related, the substantial variability about preferred modes *within* either gait category cannot be explained simply by differences in speed, especially during symmetrical gaits.

Kinematics

Chimpanzees "overstride" during symmetrical gaits, thus avoiding ipsilateral limb interference by placing one hindlimb outside its corresponding forelimb and the other hindlimb inside its corresponding forelimb. To some extent this is true of all primates (and of some nonprimate mammals when trotting), but overstriding is most pronounced in the great apes (Hildebrand, 1967). In fact in chimpanzees, "inside" vs. "outside" limbs have been shown to be asymmetrical with respect to vertical forces, propulsive impulses, muscle recruitment pat-

terns, stride length, and timing of footfalls (Hildebrand, 1967, 1968, 1976; Reynolds, 1985; Larson and Stern, 1987; Demes et al., 1994). Therefore, we tested whether or not these kinematic differences produce associated differences in preferred phase interval values (Fig. 4). In both chimpanzees, overlap of phase interval values for inside vs. outside hindlimbs is extensive. Nevertheless, the differences in phase intervals due to hindlimb placement are significant for Chimpanzee 1 ($P < 0.01$) but not for Chimpanzee 2. Therefore, chimpanzee-specific phase interval patterns may in fact be influenced by overstriding style, but given the lack of significant differences in Chimpanzee 2, data from other individuals would be necessary to verify this conclusion.

DISCUSSION AND CONCLUSIONS

In chimpanzees, as previously reported for *Lemur* and *Miopithecus* (Fig. 5) (Jungers

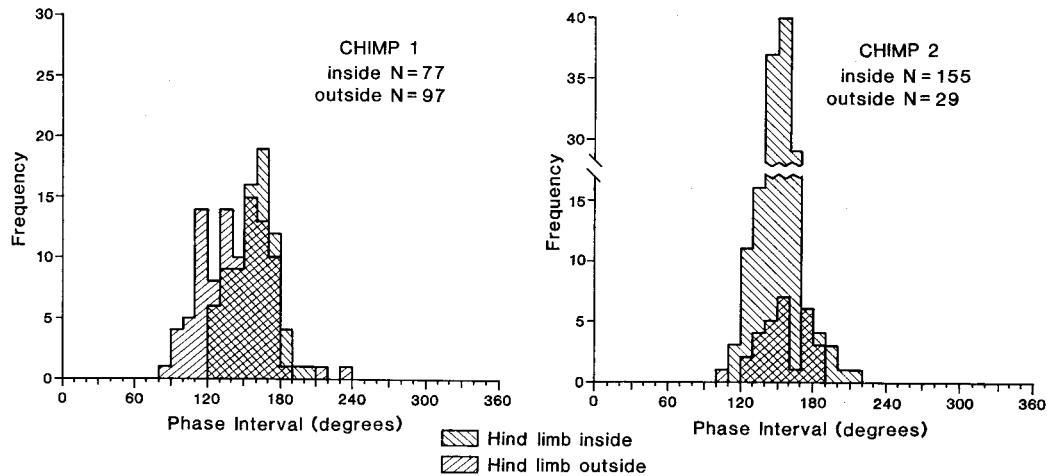


Fig. 4. Frequency distributions of phase intervals for the two chimpanzees, separated by kinematic preferences for "overstriding." Phase interval distributions of "inside" vs. "outside" hindlimbs differ significantly in Chimpanzee 1. The data represent symmetrical gaits only.

and Anapol, 1985), a "preferred," or most frequently used phase interval appears to be associated with both symmetrical and asymmetrical gaits, although variability (not related to speed) surrounds the preferred intervals. These observations reflect the neurological constraints placed on locomotion but also emphasize the overall flexibility of locomotor neural mechanisms (English, 1979). In other words, the variability around a preferred phase interval may be a reflection of an animal's necessity to respond to changing environmental cues as well as intrinsic adjustments (Coss et al., 1978; English, 1979; Pearson, 1987; Harris-Warwick and Johnson, 1989; Smith et al., 1993).

This study also indicates that interlimb coordination patterns are species-specific, both within primates and between primates and cats. During symmetrical gaits, all three primates (chimpanzee, talapoin monkey, and lemur) differ significantly with respect to their phase interval distributions ($P < 0.05$), with the "central tendency" of *Miopithecus* approximately intermediate with respect to those of the lemur and chimpanzee (Figs. 2, 5). These interspecific differences might be suggestive of phylogenetic differences in the neural control of locomotion, since the chimpanzees' distributions are more similar in central tendency to that of the other anthropoid (*Miopithecus*) than to that of the pro-

simian (i.e., the most frequent values are 110–130° in *Lemur*; 120–130°/140–150° in *Miopithecus*, and 150–170° in *Pan*). Differences between the chimpanzee and the other two primates might also be related somehow to the more exaggerated overstriding used by the chimpanzees. Moreover, as Hildebrand (1968) demonstrated in his analysis of symmetrical gaits among various breeds of domestic dogs, differences in preferred phase intervals among primates may be a reflection of differences in body size or shape (e.g., limb proportions). Indeed, relative limb lengths of the chimpanzee, talapoin monkey, and lemur vary strikingly (Jungers and Susman, 1984; Jungers, 1985).

Chimpanzees exhibit less variability during galloping than either the lemur or talapoin monkey (Figs. 2, 5). In addition, the chimpanzees utilized longer phase durations during galloping than did the other two primates (compare Fig. 3 to figs. 3 and 5 in Jungers and Anapol, 1985). For the larger-bodied chimpanzees, the experimental enclosure provided relatively less space for galloping. Whether or not these factors are somehow responsible for the less variable distributions of phase intervals in the chimpanzees has not been determined.

Interlimb coordination patterns in the chimpanzee, lemur, and talapoin monkey can also be compared to those exhibited by

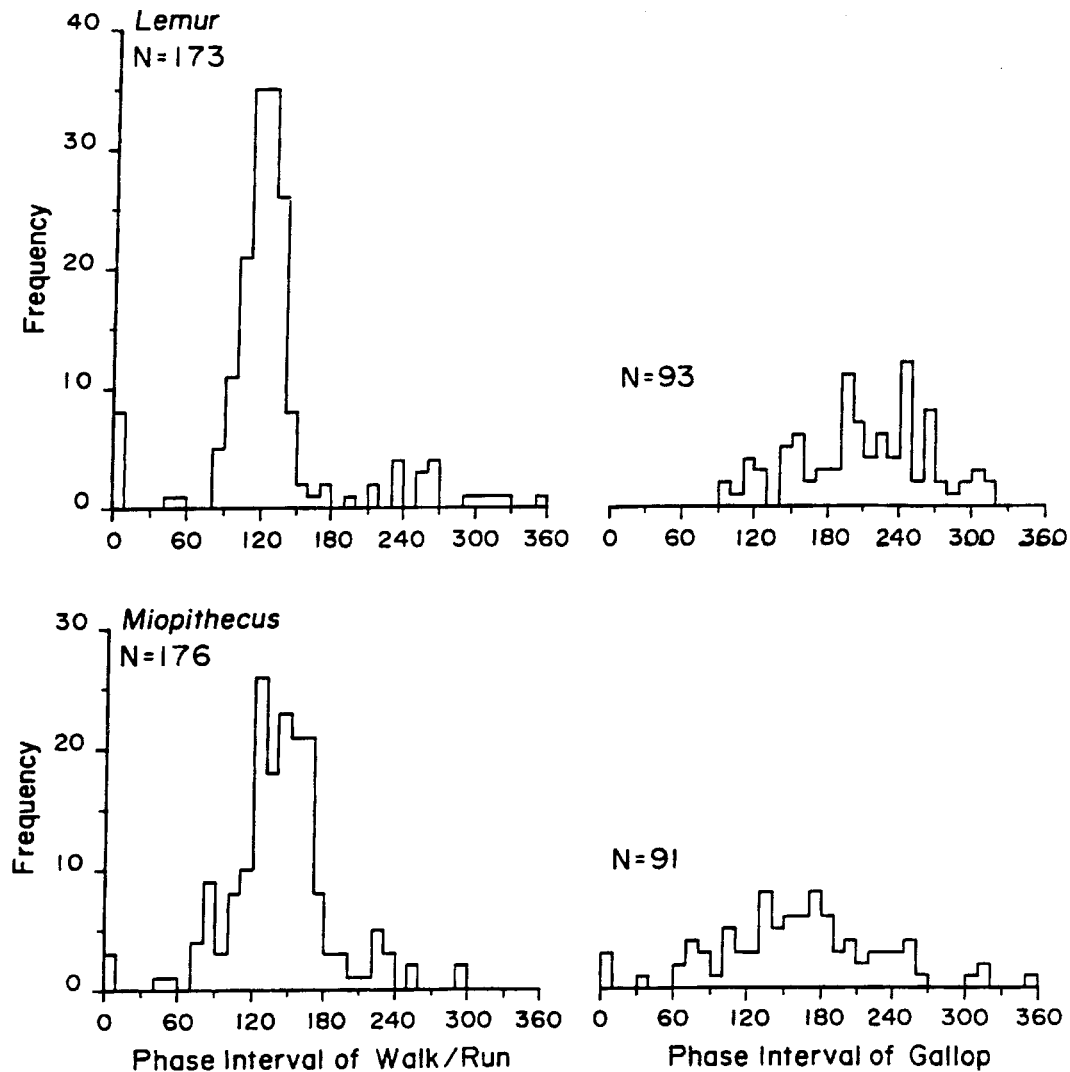


Fig. 5. Frequency distributions of phase intervals for *Lemur* and *Miopithecus* during symmetrical (walk/run) and asymmetrical (gallop) gaits reported by Jungers and Anapol (1985). Compare to chimpanzee data in Figure 2. Patterns of interlimb coupling vary clearly with gait in all three primates, as well as by species. See text for details.

the cat. Our results are generally consistent with those of Coss et al. (1978) who found that independent of speed, cats use a range of ipsilateral interlimb timing intervals within both symmetrical (walk, trot) and asymmetrical gaits (gallop). Similarly, English (1979) found variability around a preferred phase interval of 180° when cats used a trot (which differs significantly from the values for symmetrical gaits in primates; $P < 0.01$). However, despite his cats' general

"preference" for ipsilateral intervals of 180° at more than one speed, English did find that lower speeds (i.e., higher duty factors) appeared to be associated with phase intervals of 120° or 240°. Because English did not separate phase intervals according to gait category, we cannot ascertain whether these values represent (speed-related) variability within a gait, or a shift to a different gait, nor can we conclude that cats prefer the 180° phase interval at "all gaits and speeds"

(contra Jungers and Anapol, 1985). Nevertheless, most of English's cats exhibited a clear preference for trotting. In this sense, primates are distinct from cats because primates do not use a (running) trot (Hildebrand, 1967; Dagg, 1973; Jungers et al., 1980; Vilensky and Patrick, 1985; Vilensky, 1987, 1989).

Overall, a comparison of primates to cats reveals two main conclusions: (1) within gaits, both primates and cats have preferred but variable patterns of interlimb coordination, and (2) unlike cats, none of the primates exhibits a modal phase interval of 180° , which is consistent with the fact that primates do not use a running trot.

The EMG-derived phase interval values reported here for primates are comparable to Hildebrand's unifying scheme for symmetrical gaits based on footfall timing (Hildebrand, 1966, 1967). In Hildebrand's scheme, the hindfoot is the reference point and ipsilateral phase intervals range from 0 to 100% (i.e., the percentage of the stride that the fore footfall follows the ipsilateral hind footfall). For example, a trot is 50% in his graph and 180° in EMG phase intervals. When our EMG-derived phase intervals are translated into Hildebrand's scheme, the primate values fall within the range of values designated by Hildebrand as diagonal sequence/diagonal couplets. A diagonal sequence/diagonal couplets gait, rare among other mammals, is typical of most primates notwithstanding some flexibility (Hildebrand, 1967; Hurov, 1985; Vilensky, 1987, 1989; Vilensky and Larson, 1989). By contrast, Hildebrand's values for felids fall within ranges designated as either lateral sequence (walking) or trotting (faster speeds) (Hildebrand, 1976). Therefore, the EMG-derived phase intervals reported here are a good reflection of the uncommon walking gait of primates as well as their lack of true trotting.

Whether derived from footfall sequences or EMG data, interlimb coordination patterns in primates are clearly recognizable and, to some extent, predictable. As do cats, primates maintain preferred modes of limb timing during quadrupedal locomotion while maintaining the flexibility necessary to respond to changing demands on the locomotor

system. Therefore, although the evolution of primate nervous systems may have included increasing dominance of cerebral mechanisms over spinal CPGs (Tuttle et al., 1979; Eidelberg et al., 1981; Vilensky and Larson, 1989), our findings point to the maintenance of preferred stepping programs in quadrupedal primates, including the chimpanzee. In other words, preferred intervals within gaits and species-specific patterns of interlimb coordination among primates indicate that their locomotion remains constrained by the central nervous system.

Although our results demonstrate a notable degree of divergence in limb coordination patterns among primates and between primates and cats, other electromyographic data are more suggestive of evolutionary neuromotor conservatism (Peters and Goslow, 1983; Smith, 1994). That is, despite the distinct differences in musculoskeletal configurations and gait preferences exhibited by primates vs. cats, the activity patterns of their hindlimb and back muscles are generally comparable (e.g., Jungers et al., 1983; Vangor and Wells, 1983; Shapiro and Jungers, 1994; but see Okada et al., 1978; Jungers et al., 1980).

In contrast, unique aspects of forelimb muscle recruitment patterns in primates have been used to support the hypothesis of a change in locomotor neural circuitry (and perhaps concomitant shift to diagonal sequence gaits) that occurred with the evolution of primates. This change is thought to have been associated with the superior manipulative abilities of primate forelimbs (Larson and Stern, 1987, 1989; Vilensky, 1987, 1989; Vilensky and Larson, 1989). Similarly, the differences between primates and cats in phase interval values could have a neurological basis. If this were the case, however, differences between chimpanzees and the other two primates might be more pronounced. Instead, despite the chimpanzee's greater emphasis on forelimb manipulatory function, unusual knuckle-walking form of quadrupedalism, and tendency to "overstride," its patterns of interlimb coordination cluster with those of virtually all other primates (Hildebrand, 1967), and appear to be just as "constrained" as those of the lemur

and talapoin monkey. An alternative explanation is that differences between primates and cats in limb coupling patterns are morphologically or biomechanically driven. For example, primates use a diagonal sequence footfall pattern during climbing as well as quadrupedal walking. This type of gait may provide a biomechanical advantage during climbing by controlling the "roll and yaw" of the body and maximizing the reach of the foot during lateral trunk flexion. (Muybridge, 1899; Prost, 1965, 1969). Morphological explanations have also been put forth to explain the lack of trotting in primates. For example, Dagg (1973) emphasized that trotting requires equally proportioned limbs, and a "straight and rigid" spine because propulsive forces come from diagonal limbs. Primates vary with respect to spinal rigidity/mobility (e.g., Erikson, 1963; Benton, 1967, 1974; Ankel, 1972; Cartmill and Milton, 1977; Shapiro, 1993) as well as the relative lengths of their limbs (Jungers, 1985). Therefore, Dagg's hypotheses require further testing before a morphologically based explanation for the lack of trotting in primates can be accepted (see also Vilensky and Patrick, 1985).

In conclusion, while this study demonstrates that primate locomotion is to some extent constrained by the central nervous system, it also reveals that there are interspecific differences in interlimb coordination patterns among primates, and between primates and cats. While these results do not preclude the possibility that particular aspects of primate neural circuitry are unique (and perhaps reflect phylogenetic differences), the data are also relevant to morphologically based explanations for differences in locomotion among mammals.

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